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Highlights

Deep-sea sponge aggregation occurs in area of greatest variation in temperature

There is a log-linear relationship between sponge abundance and temperature variability

Temperature variability is attributed to internal wave activity in the study area

Sponge abundance is related to long term (132 days) mean suspended particulate matter

1 The distribution of deep-sea sponge aggregations (Porifera) in relation to oceanographic processes in
2 the Faroe-Shetland Channel.

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12 Key words: internal waves; Porifera; sponge aggregations; deep-sea; marine conservation;

13

Abstract:

Deep-sea sponge aggregations have been identified as potential Vulnerable Marine Ecosystems under United Nations General Assembly Resolution 61/105. Understanding the distribution of these habitats is critical to future spatial management efforts, and central to this understanding are quantitative data on the environmental drivers of that distribution. Accumulations of large suspension feeders are hypothesised to aggregate in regions of internal wave formation. The causal link is thought to be an increase in the supply of food related to the incidence of internal waves, which results in resuspension of particulate organic matter on which the sponges feed. There is, however, almost no empirical evidence to support this hypothesis for deep-sea sponge aggregations, although there is strong circumstantial evidence. We tested the relationship between sponge density and 1) temperature range (as a measure of internal wave presence in this region), and 2) optical backscatter (a measure of particulate flux) for a known sponge aggregation in the Faroe-Shetland Channel where internal wave interaction with the slope is further well-documented. 25 benthic video transects, ranging from 422-979m water depth were conducted in the study region. 225 images were analysed and all taxa identified to morphotypes and quantified. Temperature and optical backscatter data were drawn from archived CTD data, and data from long term (4 months) and 2 seasonal short term (11 days) mooring deployments from the region. A generalised linear model was used to test the relationship between sponge density and temperature range (ΔT), and sponge density and optical backscatter. The results showed a statistically significant positive relationship between sponge density and temperature range, with the highest sponge densities occurring at depths of greatest temperature range. They showed a statistically significant positive relationship between sponge density and optical backscatter for long term and one short term seasonal deployment (Sep-Oct), but a weak negative relationship for the other short term mooring deployment (April-May). We conclude that sponge aggregations in the Faroe-Shetland Channel are associated with slope regions that are subjected to abrupt and pronounced changes in temperature due to intensified internal wave activity over the slope between depths of 400-600 and that lead to intensified near-bed currents and elevated resuspension of particulate. Our data provide empirical evidence of the relationship between internal wave processes and deep-sea sponge

41 aggregations. These data modify current theory on drivers of deep sea sponge aggregation
42 distribution, suggesting aggregations also occur directly within regions of internal wave breaking,
43 rather than simply proximal to these regions.

44

45 1. Introduction

46 Deep-sea sponge aggregations are communities of large sponges that form under specific biological,
47 hydrological and geological conditions (Hogg *et al.,* 2010). They are a global phenomenon (Van Soest
48 *et al.,* 2012), examples of which include: *Pheronema* (formerly known as *Holtenia*) grounds
49 characterised by *Pheronema carpenteri* (Thomson, 1869) in the NE Atlantic (Rice *et al.*, 1990), dense
50 Hexactinellid reefs found off the coast of British Columbia, Canada (Krautter *et al.,* 2001) and ostur
51 grounds characterised by large demosponges on the Faroese slope and shelf (Klitgaard & Tendal,
52 2004; Murillo *et al*., 2018). Deep-sea sponge aggregations have been identified as potential
53 Vulnerable Marine Ecosystems (VME) (UNGA Res. 61/105) under the FAO's guidelines for the
54 management of deep-sea fisheries (FAO, 2009), and are listed under the OSPAR Convention as a
55 threatened and declining habitat (OSPAR, 2010). Furthermore, a recent Convention on Biological
56 Diversity (CBD) Decision XX/4 emphasised the ecological importance and sensitivity of these
57 aggregations and the need to study and conserve them; and the United Nations Environment
58 Programme have called for international engagement in mapping and modelling sponge distribution
59 (Hogg *et al.,* 2010).

60 Effective management and conservation of these habitats relies on a firm understanding of
61 their spatial distribution. While there are a number of growing datasets on the presence of individual
62 sponge taxa, data on the presence of sponge aggregations is limited, and so recent studies have
63 attempted to predict their distribution using habitat suitability modelling approaches (Knudby *et al.,*
64 2013; Ross & Howell, 2013; Howell *et al.,* 2016). The construction of models requires data on the
65 presence / absence / abundance of a species and spatial layers of data on relevant environmental
66 parameters. Models can then be developed that formalise the relationship between species presence /

absence / abundance and the environmental drivers (or surrogates for those drivers) of their distribution within a statistical framework. However, questions remain around the accuracy and reliability of modelled maps, particularly where there is only a very basic understanding of the underlying ecology and environmental drivers of species distributions (Howell *et al.,* 2016).

The distribution of deep-sea sponge aggregations is thought to be related to the interaction of internal waves (IWs) with sloping boundaries, typically the continental slope (Rice *et al.,* 1990; Kittgaard *et al.,* 1997; White, 2003) and raised features like the Mid-Atlantic Ridge (van Haren et al., 2017). Rice *et al.* (1990) postulated that accumulations of hexactinellid sponges in the Porcupine Seabight (NE Atlantic) aggregated near regions with a critical slope where the bottom slope matches the slope of propagation of internal tidal waves and near-bed currents are intensified. The causal link was suggested to be an increase in the supply of food related to the occurrence of the internal waves. Sponges are filter-feeders and represent an important link between carbon in the water column in the form of ultraplankton (2-20µm) and picoplankton (<2µm) (Reiswig, 1975), dissolved organic carbon (Yahel *et al.*, 2003; de Goeij *et al.*, 2008) and potentially viral particles (Hadas *et al*., 2006), and the benthos. Rice et al's hypothesis was extended by Klitgaard *et al.* (1997) for aggregations characterised by the demosponge Geodia spp, who put forward two mechanisms by which food availability in the form of suspended material might be increased: 1) increased primary production where internal wave mixing promotes nutrient flux to the surface, and 2) leakage of food-particle rich water from the bottom-mixed layer to the stratified ocean interior. To date there has been no formal testing of this hypothesis.

Within the Faroe-Shetland Channel (FSC) sponge aggregations are known to occur on shelf areas around the Faroe Islands (Klitgaard & Tendal, 2004) as well as on the continental slope west of the Shetland Islands (Bett, 2001). These sponge aggregations have been classified as 'Boreal Ostur' (Klitgaard & Tendal, 2004). They are characterised by sponges of the genus Geodia, specifically *Geodia barretti* (Bowerbank 1858), *G. macandrewi* (Bowerbank 1858), *G. atlantica* (Stephens, 1915) and *G. phlegraei* (Sollas 1880).

93 The FSC is also a site with particularly intense IW processes (Van Raaphorst *et al.*, 2001;
94 Hosegood *et al.,* 2004) that result in dramatic short-term changes in temperature (Hosegood, 2004a,
95 b). In addition to the generation of internal tides at a semidiurnal frequency throughout the channel
96 (Hosegood & van Haren, 2006; Hall et al., 2011), resuspension may be promoted by the propagation
97 of 'solibores' up the continental slope. Defined as features that resemble both internal bores and
98 nonlinear internal wave trains, solibores have been observed to generate a temperature decrease of
99 >4°C in less than one minute at a depth of 470 m. In the FSC, particulate fluxes are two orders of
100 magnitude larger than background levels for 2 days following the passage of solibores (Hosegood et
101 al., 2004a). Key to their generation, and the continuous critical reflection of the internal tide over the
102 slope that occurs further to the south in the FSC and generates similar near-bed intensified currents
103 (Hall et al., 2011), is the intersection of the strongly stratified permanent pycnocline over the Shetland
104 slope at depths of 400-600 m. Separating the poleward flowing surface waters of Atlantic origin and
105 the equatorward flowing waters of polar origin, the pycnocline persistently renders the slope critical to
106 internal wave reflection at the depth where it intersects the bottom, but whose location varies over
107 time due to tidal, and lower frequency, modulations of the current regime (Hosegood & van Haren,
108 2006).

109 Within the depth range of 400-600 m in the FSC, resuspension of particulate material is thus
110 persistently driven by the internal tide whereby near-bed currents and temporal changes in
111 temperature are bottom intensified with a semidiurnal frequency. Due to changes in background
112 stratification, the signature of such resuspension in moored OBS signals is effectively switched on and
113 off at a given location due to the location of internal tide generation (Bonnin et al., 2002); as the
114 background stratification evolves in response to regional scale, subinertial forcing such as coastal
115 trapped waves (Hosegood et al., 2006), the precise depth at which the slope is critical to the
116 semidiurnal internal tide changes within the 400-600 m range (Hosegood & van Haren, 2006). The
117 FSC has thus long been a site of multidisciplinary study due to these unique biological and
118 hydrographic characteristics and is an excellent site for investigating relationships between IW
119 processes and sponge aggregations.

120 Whilst the association between ostur aggregations in this region and IW processes has been
121 suggested by previous authors (Bett, 2001; Klitgaard & Tendal, 2004), there has been no robust
122 analysis of these relationships. This study aims to consolidate our understanding of the role of IW in
123 driving the distribution of ostur in the FSC, contributing to the development of more complex habitat
124 suitability models and a deeper understanding of how this valuable and threatened ecosystem is
125 generated and sustained. Our hypotheses are: H1 – The abundance of sponges is associated with the
126 generation of internal waves at the slope, H2 – The abundance of sponges is related to the amount of
127 particulate matter in suspension.

128

129 ## 2. Methods

130 ### 2.1 Study Area

131 The FSC is a roughly symmetrical, widening trench bounded by the Faroe Islands in the west and the
132 Shetland Islands in the east (Fig. 1). It has a roughly southwest to northeast orientation. In the
133 southwest the channel terminates in sills at a depth of 850m and 500m at the Faroe Bank Channel and
134 Wyville-Thomson Ridge, respectively. To the Northeast the FSC meets the Norwegian Sea at between
135 1500-2000m (Van Raaphorst *et al.,* 2001). The hydrography of the FSC is primarily underpinned by
136 the constituents of the water column, which comprises 5 distinct water masses described in Turrell *et*
137 *al.* (1999).

138

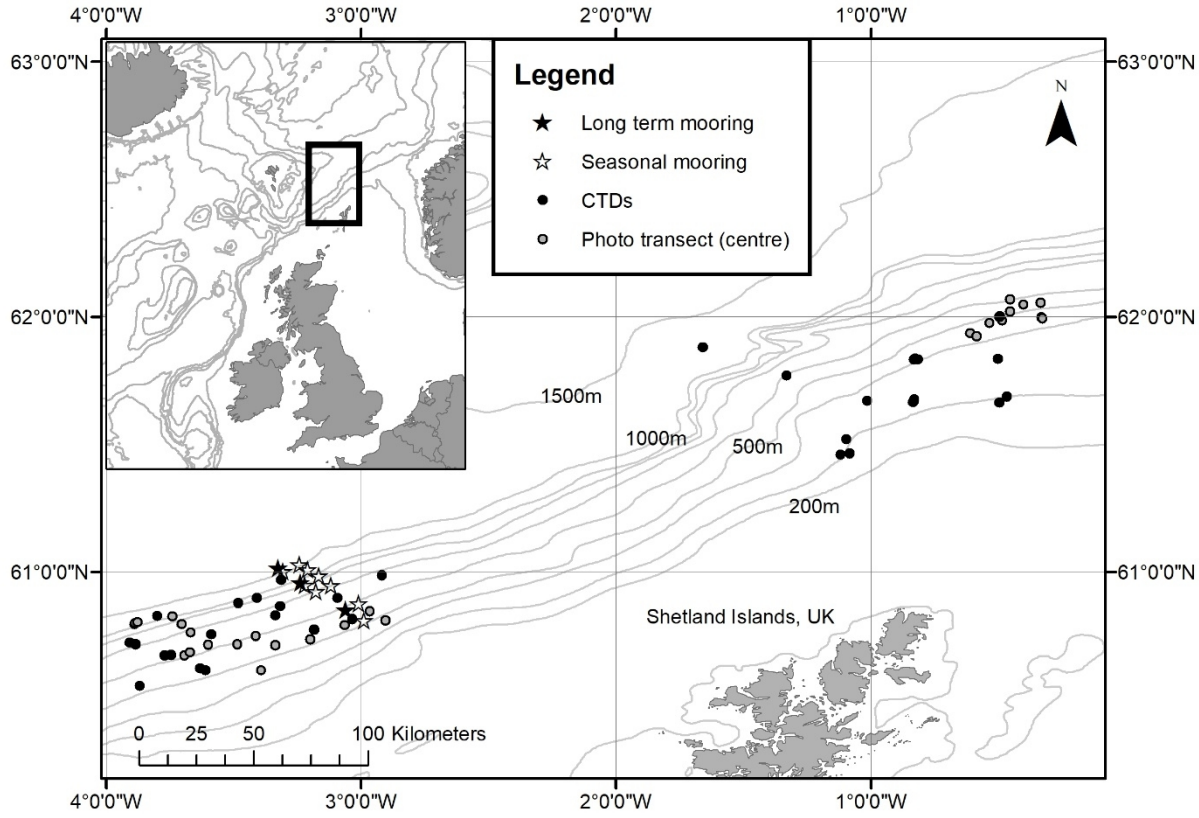


Figure 1: Map of the Faroe-Shetland Channel detailing the locations of areas of study, CTD casts, image transects (mid point shown), and PROCS-1-3 mooring sites, North of Scotland, Shetland and Orkney shown in grey.

2.2 Biological Data

Biological data were derived from 25 benthic video / image transects conducted by the M/V Franklin during the combined Strategic Environment Assessment 7/ Special Area for Conservation survey in 2006 (Jacobs & Howell, 2007). Transects were conducted on two separate sites; FSC_NE *(n=9) (62°00-00'N, 1°00-00'W)* and FSC_SW *(n=16)* (*61°00-00'N, 3°30-00'W)* (Fig. 1) and ranged from 473m to 2591m in length. Sea-floor image data were collected with the SEATRONICS drop frame camera system (Howell *et al.,* 2010). The system comprised an integrated DTS 6000 digital video telemetry system, which provided a real time video link to the surface, a digital stills camera (5 mega pixel, Kongsberg OE14-208) and a colour video camera (Kongsberg OE14-366). The stills camera

153 was mounted at an oblique angle (22º) to the seabed. Sensors monitored depth, altitude and
154 temperature, and an Ultra Short Base Line (USBL) beacon provided position data accurate to 1m
155 (Howell et al., 2007). The drop frame was towed in the water column between one and three metres
156 above the seabed. At approximately 1 minute intervals the camera was landed on the seabed and a still
157 image taken. This ensured a consistent size field of view for images.

158 For each transect 9 images were quasi-randomly selected for analysis, giving 225 images for analysis.
159 Compromised images (e.g. high sediment, large obstructions, resolution or contrast issues) were
160 omitted and an alternative image selected. Selected images were quantitatively analysed in the
161 following manner: all sponges >1cm were identified and counted, percentage cover of sponges was
162 also calculated using a calibrated grid superimposed over the image (data were rounded to the nearest
163 0.25 of a grid square). Sponge taxa were identified as distinct Operational Taxonomic Units (OTUs)
164 following Howell & Davies (2010). OTUs may not conform to established taxonomy. Sponge OTUs
165 were defined by colour, shape, and specific terminology found within Ackers *et al.* (2007) and
166 grouped into distinct morphologically similar groups as a result of the difficulty in identifying
167 sponges using images. Image data were then pooled by transect.

168

169 2.3 Oceanographic Data

170 Variation in the temperature range with depth was chosen as an indicator for the presence of internal
171 waves at the seabed as recorded by Nansen (1902). Archived CTD casts for the immediate region of
172 study (FSC_NE = 18n, FSC_SW = 18n) were obtained from the British Oceanographic Data Centre
173 (BODC) (Fig. 1). The CTD profiles all reach to within approximately 10 m of the sea bed. These data
174 spanned a period of 28 years (1984-2012). Mean, range and standard deviation were calculated for
175 temperature (°C) at 20m depth intervals from all CTD casts *(n=36)* from 0-1300m (Supplementary
176 material, Fig. S1). These data are considered low temporal resolution data and will be referred to as
177 such henceforth.

178

179 Higher resolution data on temperature, and data on turbidity (optical back scatter, (OBS)) were
180 obtained from moorings deployed over the Shetland continental slope by the Royal Netherlands
181 Institute of Sea Research (NIOZ) during the 'Processes on the Continental Slope' (PROCS)
182 programme (Fig. 1). Medium temporal resolution data (hereinafter referred to as PROCS-2 data) were
183 derived from three 'long term' moorings deployed for a period of 132 days (May – Sept 1999) at 552,
184 803, 1043m depth. Temperature and optical backscatter were recorded hourly. In addition seasonal
185 high temporal resolution data were obtained from two further sets of moorings deployed for an 11 day
186 period in April-May (PROCS-1 research cruise, 4 moorings at 471, 700, 777, 1000m) and Sept-Oct
187 (PROCS-3 research cruise, 5 moorings at 550, 700, 800, 900, 1000m) (Fig. 2). Temperature and
188 optical back scatter was logged every 4 mins.

189

190 Optical backscatter was measured using a Seapoint STM optical backscatter sensor (OBS). Optical
191 backscatter indicates the presence of suspended particulate matter with the limitation that the raw
192 signal (measured in Volts, with a higher voltage indicating a greater proportion of suspended
193 particles) depends heavily on the particle size in accordance with Bunt et al., (1999), who found that
194 optical devices are most sensitive to particles <20µm in diameter. The OBS in this study is capable of
195 detecting particles in the ultra and picoplankton size range (size fraction on plankton known to be
196 utilised by sponges as a food resource), but it must be noted that OBS is a bulk measure of suspended
197 material and its use here as a proxy for availability of potential food resource for sponges is limited
198 and this is acknowledged in the discussion.

199

200 For medium and high resolution moorings data mean, range and standard deviation were calculated
201 for temperature (°C) and OBS over the full deployment period for each mooring. To investigate the
202 relationship between sponge abundance and temperature variation / OBS, each photo transect was
203 paired with the nearest mooring from each of the PROCS1, PROCS2 and PROCS3 datasets.

204

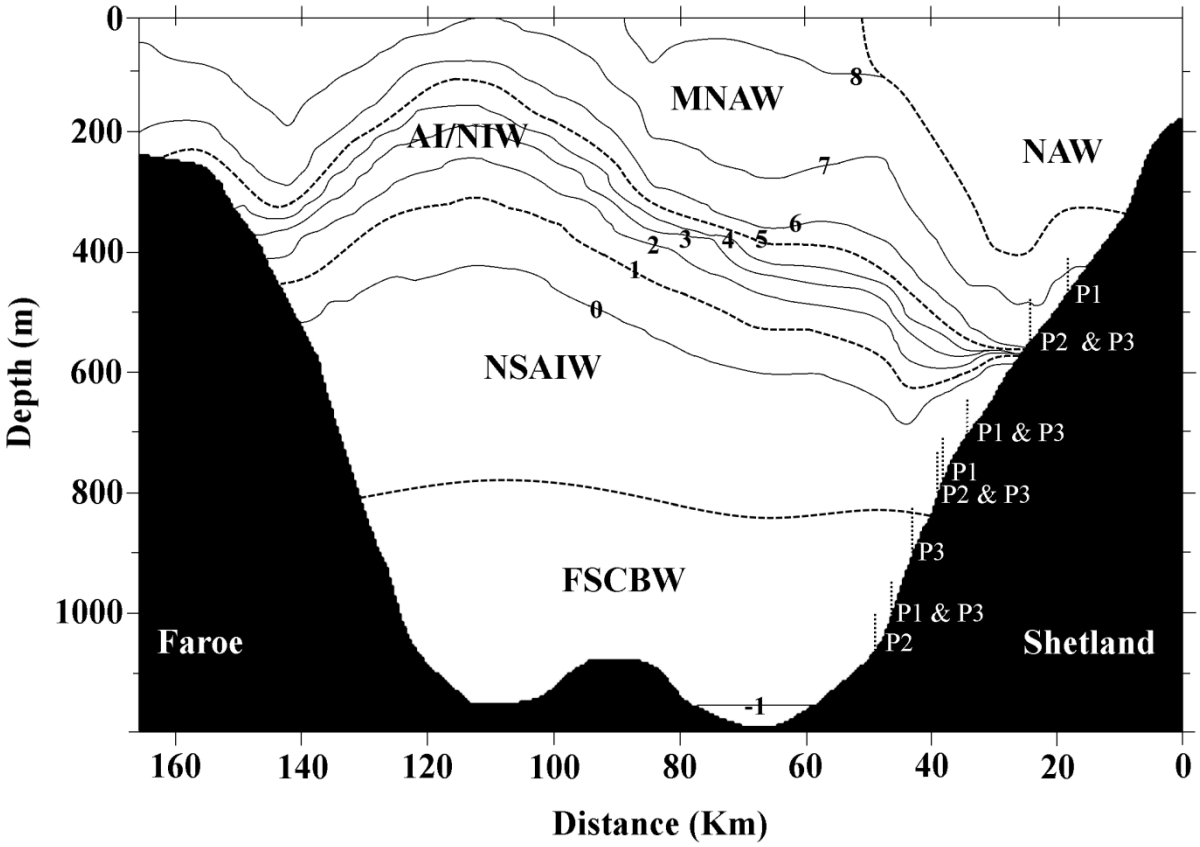


Figure 2: Cross section of the Faroe-Shetland Channel showing detailed temperature and water masses as described by Turrell et al. (1999). PROCS-1-3 (P1-3) mooring depths are indicated by vertical dashed lines. Numbers 0-8 are isotherms in °C; water masses are North Atlantic Water, Modified North Atlantic Water, Arctic Intermediate / North Icelandic Water, Norwegian Sea Arctic Intermediate Water, Faroe-Shetland Channel Bottom Water (Redrawn from Hosegood, 2005).

2.4 Statistical Analysis

Preliminary analysis demonstrated that temperature range data (ΔT) from CTDs, long term and short term moorings were highly correlated therefore only CTD data were used in further analyses. In addition, sponge abundance and sponge percent cover were highly correlated (Kendall's Rank (Tau) $T = 0.646$, $P<0.001$) and so only sponge abundance was used in further analyses. Scatter plots of sponge abundance vs temperature range suggested a log-linear or polynomial relationship was present. Simple linear, log linear and polynomial models were fitted to the data, however a log-linear model

219 provided the best fit and explained substantially more variance than other models trialled. To test H1 a
220 linear model was used to test for a significant relationship between log sponge abundance and ΔT
221 from archived CTD data.

222 Scatter plots of sponge abundance vs OBS again suggested a log-linear or polynomial relationship
223 was present between sponge abundance and OBS. However, the limited data available for OBS from
224 only 3 or 4 moorings (depending on whether long term or seasonal datsets) meant it was inappropriate
225 to fit a model to these datasets. Instead for long term (PROCS-2) data, sponge abundance data were
226 grouped by mooring (OBS) and a Kruskal–Wallis test was used to test for a significant differences
227 in sponge abundance between moorings and thus long term (PROCS-2) OBS data. The relationship
228 between sponge abundance and short term seasonal (PROCS-1 and PROCS-3) OBS data were not
229 formally tested but are described.. Data analysis was conducted using R-Studio (RStudio Team, 2016)
230 a wrapper for the program R (version 3.3.2 (R Core Team, 2016)).

231

232 3. Results

233 3.1 Sponge abundance and variation in temperature (indicative of the influence of internal waves)

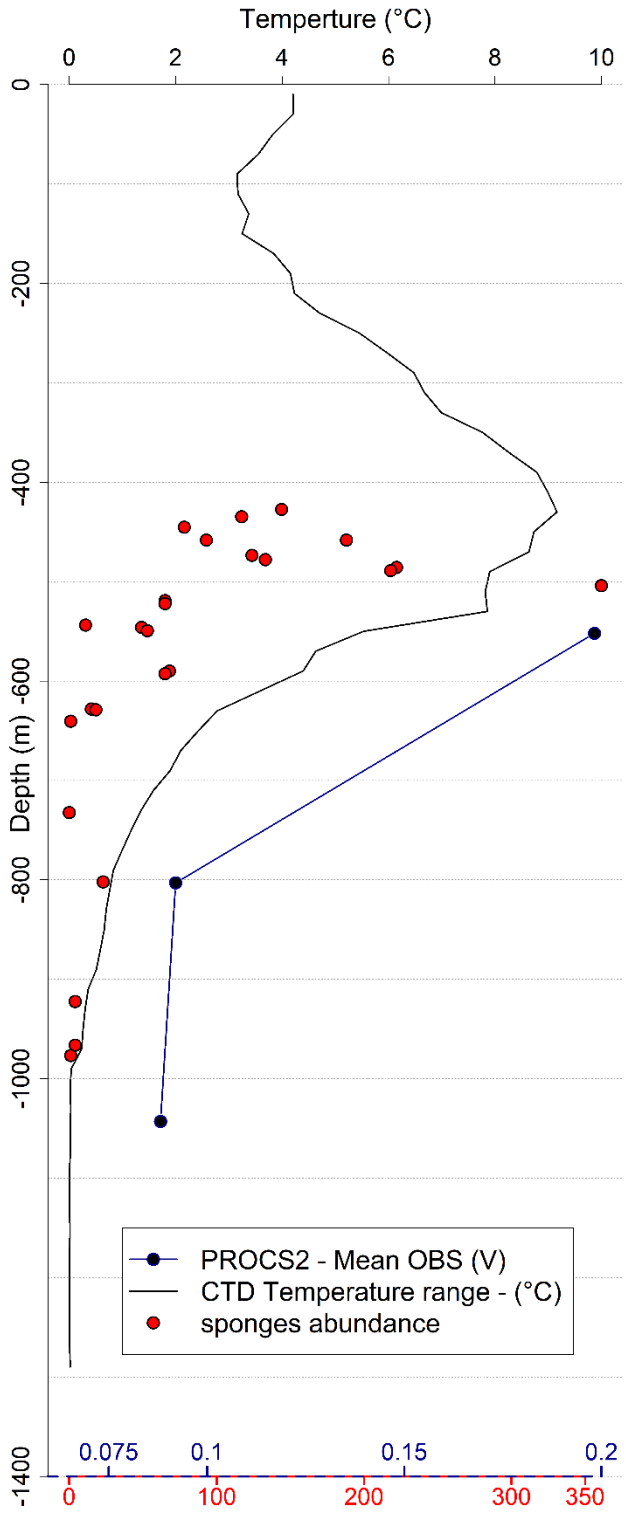
234 ΔT for all datasets peaked between 400 and 600m, with a maximum range of around 9ºC (Fig. 3, Fig.
235 S1). Sponge abundance peaked at approximately 500m (498m =361 individuals), and transects with
236 the highest recorded abundances were all located between ~400-600m (Fig. 3). Sponge abundance
237 declines rapidly deeper than 600m. There is a highly significant linear relationship between log
238 sponge abundance and ΔT ($p < 0.001$, Multiple R-squared: 0.73 on 23 df, Supplementary material,
239 Fig. S2).

240 3.2 Sponge abundance and the resuspension of particulate material

241 Box plots of mean long term OBS data (PROCS-2) appeared to show a log-linear relationship with
242 sponge abundance although this was not formally tested as a result of limited data. A Kruskal–Wallis
243 test confirmed there was a significant difference in sponge abundance between moorings and
244 therefore low, medium, and high OBS values (p-value = 0.01238). These data suggest that sponge

245 abundance is related to mean long term particulate resuspension at the seabed (Fig. 3) However, the
246 data are confounded by depth, and have limited resolution as photo transect data have been assigned
247 to the nearest mooring, and data are only available from 3 moorings (Supplementary material Fig.
248 S3). High resolution seasonal data for Sept-Oct (PROCS-3) appeared to have a positive log-linear
249 relationship with sponge abundance, however seasonal data for April-May (PROCS-1) showed a
250 more complex relationship with sponge abundance, where sponges abundance was low at very high
251 OBS values (Supplementary material Fig. S4). This suggests that sponge abundance has a more
252 complex relationship with short term seasonal observations of OBS. However, again it must be
253 considered that data are only available from 4 moorings.

254



255

256 Figure 3: Sponge abundance determined from pooled image data by transect, temperature variation

257 (ΔT) from CTD casts, and long term optical backscatter (PROCS-2) as a function of depth.

258

4. Discussion

4.1 Sponge abundance and temperature variations

Large temperature changes are observed between 400-600m depth in this region of the FSC which, on the basis of previous studies, are attributed to internal wave activity (Fig. 3). This depth-range is consistent with the established critical slope angle for internal semi-diurnal tidal waves (M_2 waves), calculated to be 350-550m on the SE slope of the FSC (Van Raaphorst *et al.,* 2001) but also the depth range over which solibores propagate up, and along, the slope (Hosegood et al., 2004b). The highest densities of sponges are also located at between 400-600m, and our results suggest there is a significant linear relationship between temperature range and sponge abundance, suggesting that sponge abundance is highest in the region of internal wave activity at the seabed. The mechanism responsible for the generation of the solibores in this particular location have been suggested to be the nonlinear evolution of the permanent pycnocline that subsequently evolves into various forms of an internal wave train (Hosegood et al., 2006). Internal tides are not necessarily responsible but we note that Hall et al. (2011) observed dynamically similar features in the southern prion of the FSC to occur with semidiurnal frequency leading to the conclusion that the critical slopes at this depth range lead to nonlinear internal tide reflection. The common factor in either scenario is a rapid drop in temperature accompanied by intense near–bed currents.

Although in general agreement, this is contrary to the current theory, which suggests sponge aggregations are found near to, but not in, regions of internal wave breaking (Rice *et al.,* 1990; Kittgaard *et al.,* 1997; White 2003). Increased velocities associated with regions of critical slope angle and therefore internal wave propagation were postulated to be too severe for sponge species to persist (White, 2003). Sponge aggregations were postulated to form ‘downstream’ of regions of breaking internal waves, such that they benefitted from material transported by turbulent mixing but were not subject to breaking waves. In this study the highest densities of sponges were found at ~500m (Fig. 3) which corresponds well with the highest cross-slope enhancement of velocity at 502m on the SE shelf of the FSC (Van Raaphorst *et al.,* 2001). This study suggests that ostur aggregations are capable of

286 withstanding strong bottom currents. The initial theory was postulated for aggregations of *P.*
287 *carpenteri*, which grow mainly on fine sediments and weakly anchor themselves via a spicule matt
288 (Rice *et al.*, 1990). Ostur species are characteristically found physically attached to gravel, small
289 cobblestones or hard sediments (Klitgaard & Tendal, 2001). Furthermore, ostur sponges are regularly
290 found to have gravel incorporated into the cortex (Klitgaard & Tendal, 2001), which could enable
291 them to more strongly anchor to the seafloor, allowing them to resist faster current speeds.

292 The flow rate through a sponge is also dictated by the ambient flow (Vogel, 1977). *Geodia barretti*
293 (Bowerbank, 1858), a defining species of ostur grounds, has been shown, in a combination of
294 laboratory and *in situ* conditions, to have pumping rates 6 times slower than shallow water sponges
295 (Kutti *et al.,* 2013), therefore it is possible that if ostur are able to resist higher current regimes this
296 may lead to greater food acquisition. This could be achieved by increased flow through the sponge as
297 a result of the significantly enhanced bottom currents due to internal wave breaking, where peak
298 current velocities in this region can reach >75cm s-1 (Masson, 2001).

299

300 4.2 Sponge abundance and the resuspension of particulate material

301 We found significant differences in sponge abundance between areas of low, medium and high OBS,
302 and our data suggest there may be a positive log-linear relationship between sponge abundance and
303 OBS from long term mooring data as well as seasonal short term mooring data (PROCS-3), although
304 available data were insufficient to formally test this. High OBS values are indicative of high levels of
305 suspended particulate material.

306 Current theory suggests that sponge aggregations are promoted by the presence of internal waves as a
307 result of either: 1) increased primary production that may occur where internal wave mixing promotes
308 nutrient flux to the surface, or 2) leakage of food-particle rich water from the bottom-mixed layer to
309 the stratified ocean interior. Our data would suggest the latter mechanism may operate in the FSC.
310 Due to the presence of tidally driven internal waves (Van Raaphorst *et al.,* 2001; Hosegood et al.,
311 2006) and solibores generated by subinertial processes (Hosegood et al., 2004b), there is likely to be a

312 permanent intermediate nepheloid layer between the intermediate and deep water masses (Turrell *et*
313 *al.,* 1999) around 500-550m (Van Raaphorst *et al.,* 2001). This nepheloid layer could provide the
314 sponges with a sustained and reliable food source and thus support the formation of aggregations. A
315 recent study focused on sponge aggregations on the summit of an Arctic seamount also suggested
316 sponge densities were associated with elevated near-bed suspended particulate material
317 concentrations, likely as a result of local / near-field resuspension by tidal currents, the driver being
318 improving food supply to the sponges (Roberts et al., 2018). However, we do not know if the
319 resuspended material observed here is utilised by the sponges as a food source. Nor do we know the
320 nutritional value of the material to the sponge. Thus we cannot demonstrate that it is the resuspension
321 of material that drives sponge abundance through provision of food resource.

322 Although our data suggest a positive log-linear relationship between sponge abundance and OBS data
323 from long term moorings and short term seasonal moorings deployed in Sep-Oct, there is a more
324 complex, relationship between sponge abundance and OBS data from seasonal short term moorings
325 deployed in April-May when the most intense solibores were observed (Hosegood *et al.,* 2004a).

326 Within the April-May short term mooring deployment (PROCS-1) a solibore event occurred on day
327 112 during a barotropic neap tide, the period where internal tidal forcing would be expected to be the
328 weakest (Hosegood *et al.,* 2004b). Solibore events were observed to occur approximately every 4-7
329 days and are not directly associated with tidal forcing (Hosegood et al., 2004b; Hosegood et al.,
330 2006), therefore they are not likely to be reliable for frequent particulate resuspension. However,
331 during a solibore event the amount of particulate that can be resuspended is up to 100 times the
332 amount than that can be resuspended by typical steady currents (Fig. S4). During the solibore event
333 observed during PROCS-1 the total max flux at >700m was shown to be 2 orders of magnitude higher
334 than that at 470m during the day following the solibore occurrence (Hosegood et al., 2004a). Sponge
335 abundance is low at 700m where PROCS-1 seasonal OBS is highest (Supplementary material - Figure
336 S4). It is possible that this concentration of particulate matter in the water column might exceed the
337 tolerance levels for the sponges resulting in the clogging of the osculum and ostia, leading to a
338 depressed metabolism and possible mortality (Klitgaard & Tendal, 2004). It is possible that sponge

aggregations do not extend deeper in the FSC as a result of these episodic mass flux events. However, geodid sponges are able to tolerate high exposure to suspended particulate by reducing respiration rates by up to 86%, for a short time (Tjensvoll *et al.,* 2013). In addition more recent studies have shown that chronic (29 day) cyclic exposure to natural bottom sediment did not affect geodid respiration (Kutti *et al*., 2015). It is therefore more likely that the consistently lower temperatures below 600m (~0ºC) may lie outside the thermal tolerance of the sponge species observed. Species characteristic of boreal ostur, including *G. barretti*, *G. macandrewi*, *G. atlantica* and *G. phlegraei*, have been observed over a temperature range of -0.62–10.75 °C (Cardenas et al., 2013; Howell et al., 2016), with the lower figures coming from the FSC where the lower temperatures are only experienced periodically not consistently.

4.3 Further Observations and Remarks

This study has shown a significant log-linear relationship between temperature range and sponge abundance, suggesting that sponge abundance is highest in the region of internal wave activity at the seabed. If the relationship between sponge abundance and internal wave processes can be shown to be consistent across multiple sites globally, it would provide a powerful predictor in the further development and application of habitat suitability modelling approaches to predictively map the distribution of sponge aggregations in the deep sea. Our study is of one site in one basin and does not enable such a generalisation to be made. It does however provide quantitative data on the nature of that relationship at this site, such that a more comprehensive test of this relationship can be made in future.

This study has also shown that sponge aggregations of the FSC are subjected to rapid and large changes in temperature as result of the extreme thermal gradient in the FSC and the propagation and breaking of internal waves. Sites with sponge aggregations consistently experience 6°C shifts in temperature, with the highest variation being over 9°C (Supplementary material, Fig. S1)). Aggregations are frequently subjected to water <0°C due to the movement of the pycnocline, but

365 temperature varies between approximately -1 and 9ºC and is on average around 3.5ºC . Changes in
366 temperature of this magnitude might be expected to induce heat shock and possibly mortality. *G.*
367 *barretti,* a key constituent of these aggregations, has been observed to be intolerant to sustained rises
368 in temperature. Guihen *et al.* (2012) observed that 95% of specimens were killed during two heat
369 shock events in 2006 and 2008, by a 4℃ rise in temperature in <24h, which was then sustained for
370 several days. Temperatures peaked at 12.6℃. These authors suggested that 12.6℃ exceeded the
371 thermal tolerance for *G. barretti* and that observed mortality was caused by microbially induced
372 anaerobic degradation. Our data suggest that *G. barretti* is able to tolerate rapid but sustained
373 fluctuations in temperature of between -1 and 9ºC.

374

375 Interestingly a recent study from the Scotian Shelf in the Western Atlantic found that sponge grounds
376 in the Emerald Basin formed by the hexantinellid *Vazella pourtalesi* occurred in areas of historically
377 high inter-annual variability in bottom temperature and salinity (Beazley et al., 2018). Temperature
378 ranged from 4°C in the mid 1960's to upwards of 12°C in more recent years, giving a similar level of
379 shift in temperature (8°C) to that observed in this study over short time-scales. These data suggest that
380 sponge grounds may be tolerant to some level of temperature fluctuation on both short and long-term
381 time-scales. Beazley et al (2018) suggest that these types of observations can give insight into how
382 deep-sea sponge species will respond to future climate change.

383

384 5. Conclusions

385 This paper offers a formal test of the relationship between sponge aggregations and temperature
386 variation (ΔT). Large temperature changes observed between 400-600m depth in this region of the
387 FSC have been attributed to internal wave activity, and this depth-range is consistent with the
388 established critical slope angle for internal semi-diurnal tidal waves (M2 waves). While we cannot
389 rule out the involvement of other oceanographic processes in driving these variations in temperature,
390 available data suggest the abundance of sponges in the FSC is associated with the generation of

391 internal waves at the slope (H1). We have also demonstrated a relationship between sponge
392 abundance and long term (132 days) mean suspended particulate matter in support of H2. The highest
393 values of long term OBS and highest abundance of sponges also occur between 400-600m, where
394 breaking internal waves are known to resuspend particulate material. Formal testing of this
395 relationship is confounded by depth and limited data from only 3 moorings

396

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The distribution of deep-sea sponge aggregations (Porifera) in relation to oceanographic processes in the Faroe-Shetland Channel.

Joshua J. Davison, Hans van Haren, Phil Hosegood, Nils Piechaud, Kerry L. Howell.

Supplementary material

Figure S1: Temperature profiles generated from 36 CTD casts in the Faroe-Shetland Channel, temperature range was calculated in 20m depth bins.

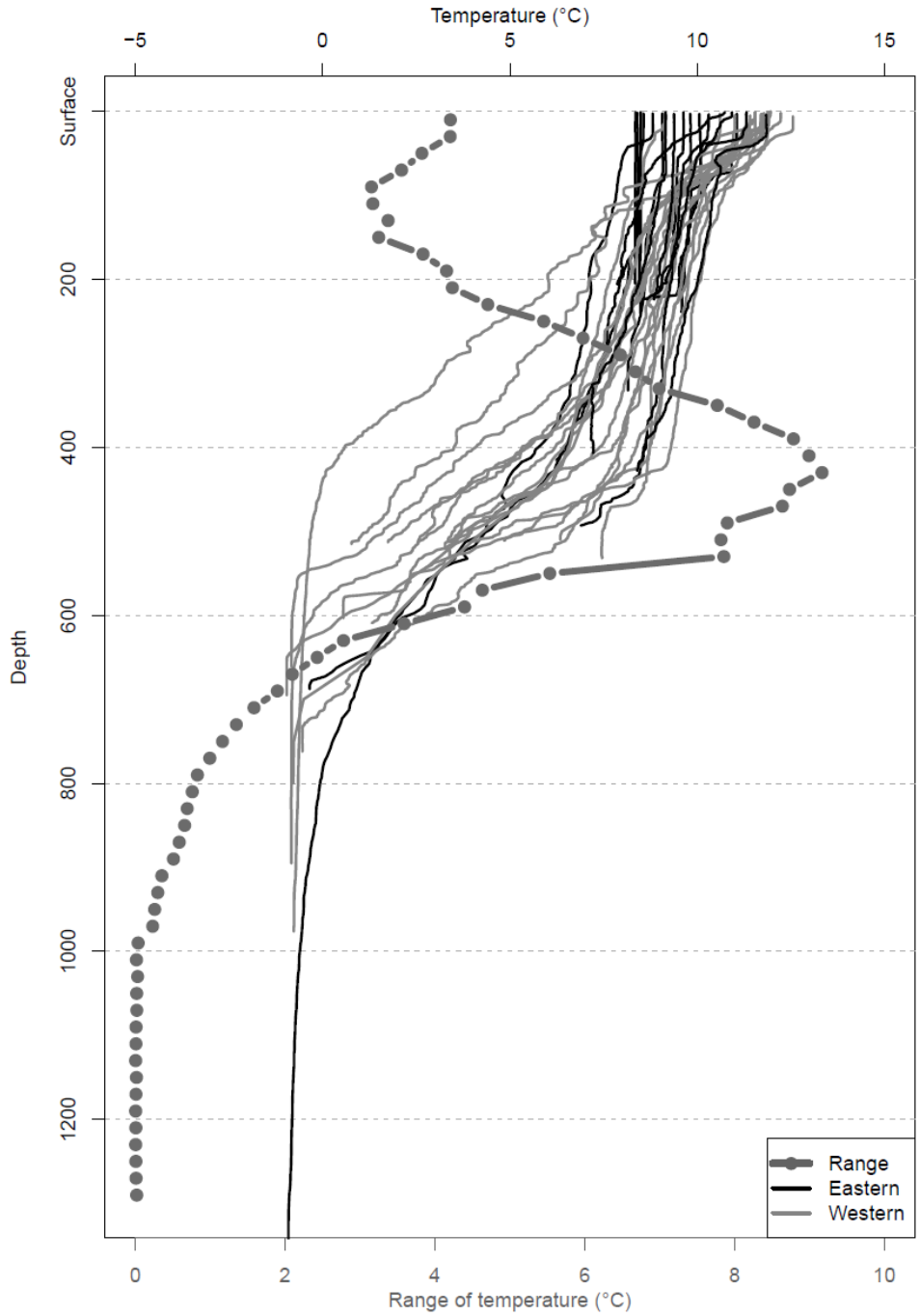
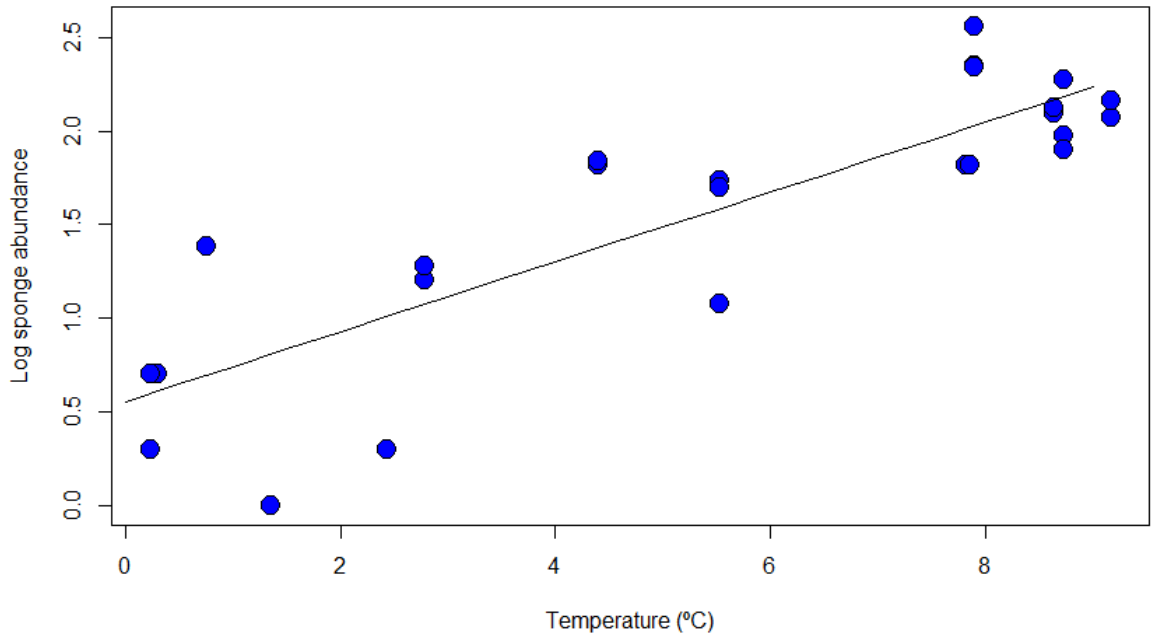
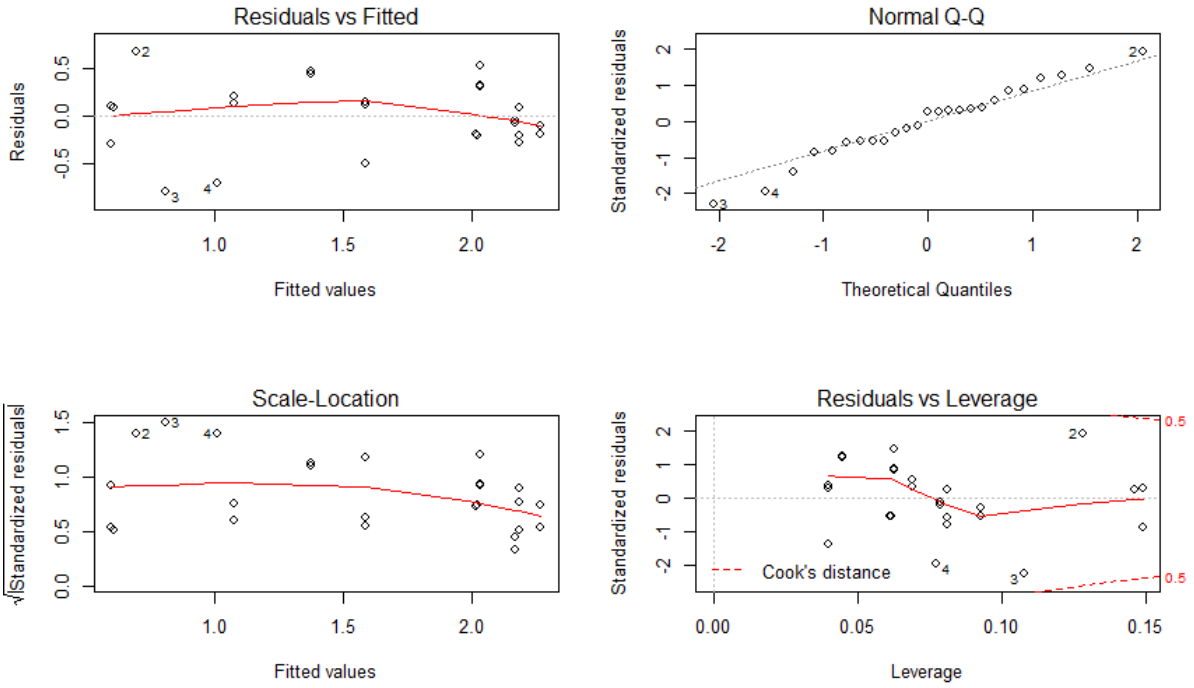


Figure S2: a) linear regression of log sponge abundance vs CTD temperature range. b) diagnostic plots






```
Raw model output

lm(formula = logAbunP1 ~ TempR, data = data)

Residuals:
```

```
     Min       1Q   Median       3Q      Max
-0.80616 -0.20192  0.08876  0.20566  0.68389

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.55398    0.14929   3.711  0.00115 **
TempR        0.18680    0.02348   7.955 4.72e-08 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.375 on 23 degrees of freedom
Multiple R-squared:  0.7334,   Adjusted R-squared:  0.7219
F-statistic: 63.29 on 1 and 23 DF,  p-value: 4.722e-08
```

Figure S3: a) Box plots showing mean sponge abundance vs long term OBS from 3 moorings deployed at different depths on the slope (PROCS-2). Low obs = 0.088 v, mooring depth 1043m, Med= 0.092 v, mooring depth 803m. High = 0.198 v, mooring depth 552m

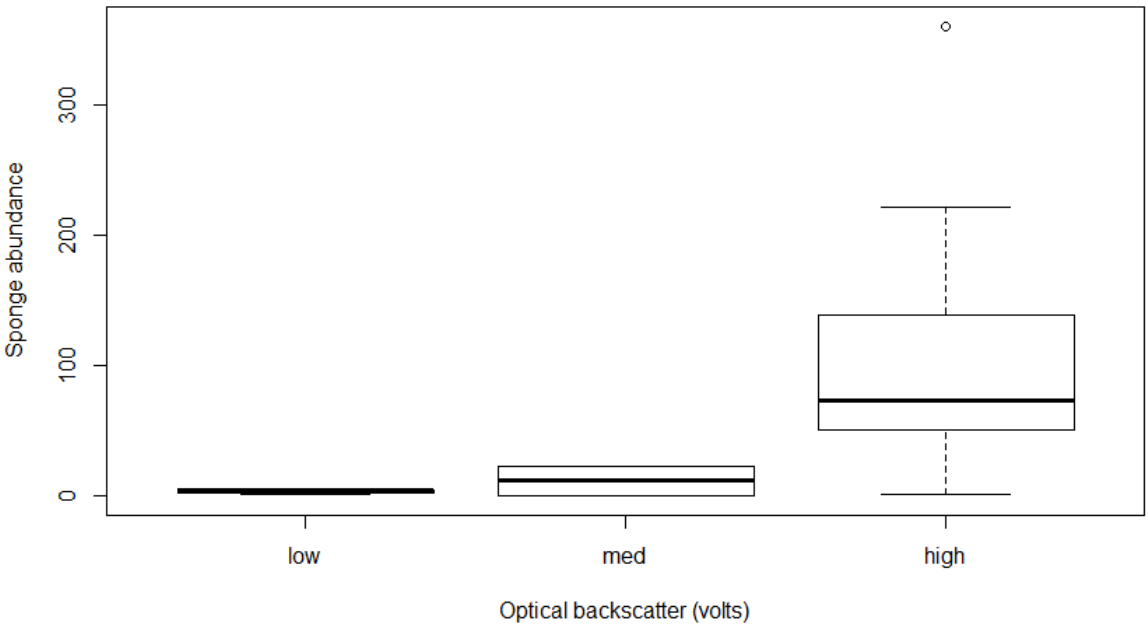


Figure S4: Sponge abundance determined from pooled image data by transect, temperature range from CTD casts, and seasonal short term optical backscatter (PROCS-1 & 3) as a function of depth.